

# A giant frog with South American affinities from the Late Cretaceous of Madagascar

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Madagascar has a diverse but mainly endemic frog fauna, the biogeographic history of which has generated intense debate, fueled by recent molecular phylogenetic analyses and the near absence of a fossil record. Here, we describe a recently discovered Late Cretaceous anuran that differs strikingly in size and morphology from extant Malagasy taxa and is unrelated either to them or to the predicted occupants of the Madagascar–Seychelles–India landmass when it separated from Africa 160 million years ago (Mya). Instead, the previously undescribed anuran is attributed to the Ceratophryinae, a clade previously considered endemic to South America. The discovery offers a rare glimpse of the anuran assemblage that occupied Madagascar before the Tertiary radiation of mantellids and microhylids that now dominate the anuran fauna. In addition, the presence of a ceratophryine provides support for a controversial paleobiogeographical model that posits physical and biotic links among Madagascar, the Indian subcontinent, and South America that persisted well into the Late Cretaceous. It also suggests that the initial radiation of hyloid anurans began earlier than proposed by some recent estimates.

Anura | Ceratophryinae | Gondwana | South America | Hyloidea

The Madagascar–Seychelles–India Plate separated from Africa  $\approx 160$  Mya and began to fragment into its component parts 88 Mya (1). Between these events, the plate was also in contact with Antarctica–Australia to the south, but the length and nature of this contact is debated (1–3). Ultimately, the Indian subcontinent continued north to contact Eurasia, and Madagascar was left 430 km from Africa, isolated by the deep Mozambique Channel (4). The remarkable diversity and endemism of the Malagasy biota has prompted intense debate as to the role of vicariance and, more recently, of dispersal in its history (5–7). The frogs of Madagascar are important to this discussion because amphibians are generally considered to be poorly suited to transoceanic dispersal (7), although exceptions are known (8, 9). In recent years, molecular phylogenetic analyses have clarified the relationships of key groups [e.g., the monophyly of Malagasy mantellids (10–13)]. Of >200 documented species, only two, the ranids *Ptychadena mascareniensis* and *Hoplobatrachus tigerinus*, are nonendemic, the latter a recent human introduction (5). The endemics are all either microhylids or mantellids, with the single exception of the hyperoliid *Heterixalus* (10). Molecular analyses have offered persuasive evidence that *Heterixalus* (14), and also *Ptychadena mascareniensis* (15), arrived from Africa in the Neogene. For these taxa, transoceanic dispersal offers the most parsimonious explanation, but the history of the endemic Malagasy mantellids and microhylids is equivocal, and both vicariant-based (7, 12, 16–18) and dispersal-based (5, 6, 19) hypotheses have been formulated. A good fossil record would aid the debate, but apart from the Triassic proanuran *Triadobatrachus* (20) and some preliminarily identified Late Cretaceous finds (21), this record has been lacking. Here we describe a very large, hyperossified anuran from the Upper Cretaceous Maevarano Formation (Fm) of Madagascar [70–65 Mya (1, 22)]. This anuran differs from extant Malagasy taxa, all of which are ranoid neobatrachians, and

instead seems to be related to South American hyloids of the clade Ceratophryinae (note that we use a standard taxonomic nomenclature (23) rather than the comprehensive, but not yet widely adopted, classification of Frost *et al.* (24)).

**Systematic Paleontology.** Systematic paleontology is as follows: Anura Rafinesque, 1815; Neobatrachia Reig, 1958; Hyloidea Ford and Cannatella 1993; Ceratophryinae Tschudi 1838; *Beelzebubfo ampinga* gen et sp nov.

**Holotype.** The holotype is as follows: fused cervical (= atlantal) and second presacral centra, Université d'Antananarivo collections, Madagascar (specimen no. UA 9600, Fig. 1).

**Etymology.** The generic name is based on *Beel'zebul* (Greek), Devil, and *Bufo* (Latin), toad, in reference to the size and probable life appearance of this anuran; the specific epithet, *ampinga* (Malagasy), means shield, in reference to cranial hyperossification.

**Locality and Horizon.** The holotype was collected from locality MAD93–25 (15° 54' 17.714" S, 46° 34' 55.946" E), Berivotra Study Area, Anembalemba Member, Maevarano Fm, Mahajanga Basin, Madagascar. The Anembalemba Member is Late Cretaceous (Maastrichtian) in age (1, 22).

**Diagnosis.** The anuran resembles adults of all extant Ceratophryinae (and differs from all other hyperossified anurans) in combining exostosed skull roofing bones, unicuspid teeth, posterolateral parietal expansion, and the absence of a projecting palatine shelf on the adult premaxilla and anterior maxilla (25, 26); it differs from all known Ceratophryinae in much larger size (estimated posterior skull widths 80–200+ mm), strong pit-and-ridge cranial sculpture, unsculptured posterior tip to the otic ramus of the squamosal, and patent cranial sutures well into maturity; it resembles extant *Ceratophrys* and *Chacophrys* in tightly interlocking maxilla-premaxilla articulation; it resembles *Ceratophrys* in having cervical cotyles continuous in ventral midline and in the possession of posttemporal fenestrae, but differs in that rostral tips of nasals fail to unite with underlying mineralized nasal cartilages; it resembles the extinct *Baurubatrachus* (27) in having pitted cranial sculpture but differs in the possession of strong ridges between pits and a more slender quadratojugal, and in much larger body size.

**Description and Comparison.** The external cranial elements of the Malagasy fossil anuran show a distinctive, coarse pit-and-ridge

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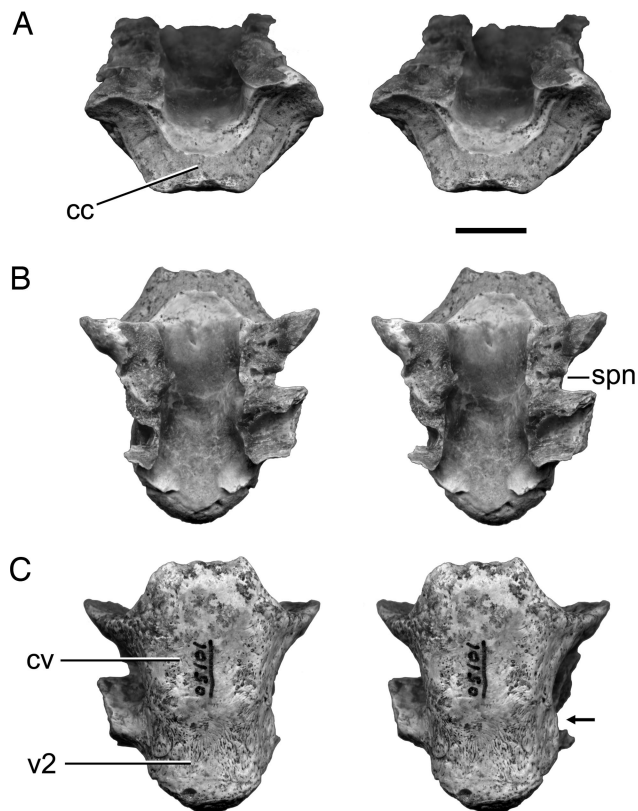
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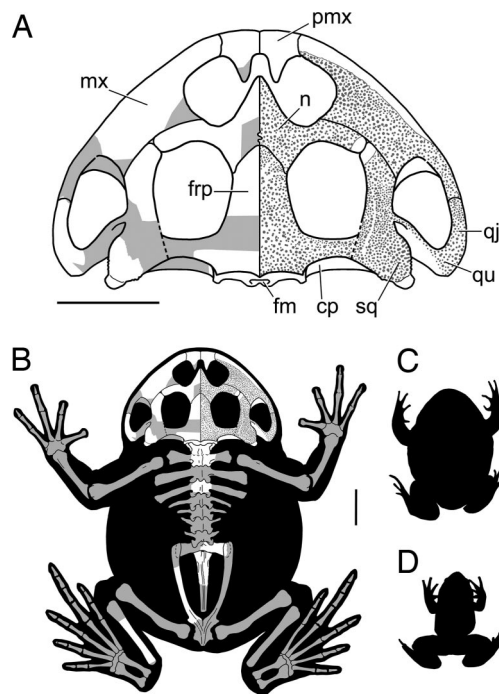
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**Fig. 1.** *Beelzebufo ampinga*, holotype, fused cervical and second presacral centra (UA 9600), stereophotographic pairs of anterodorsal (A), dorsal (B), and ventral (C) views. cc, confluent cotyles; cv, cervical vertebra; v2, second presacral vertebra; spn, spinal nerve foramen between arch pedicels. The small arrow indicates the line of central fusion. (Scale bar: 5 mm.)

sculpture that, in conjunction with the size and robustness of the bones, permits attribution of elements and is consistent with the presence of a single large hyperossified anuran species in the Maevarano Fm. Accordingly, the description and reconstruction are based on >60 bones collected from 26 localities within a 1.8-km radius [see [supporting information \(SI\) Text](#) for specimen list]. These bones include parts of all cranial roofing bones, the palatoquadrate, braincase, jaws, vertebrae, pelvis, and limb elements (Figs. 1, 2 *A* and *B*, and 3).

As reconstructed, the skull of *Beelzebufo* is wider than long (Fig. 2A), with thick, tightly sutured dermal roofing bones. The premaxillae (Fig. 3A and B) are unsclatured, but their attribution to *Beelzebufo* is confirmed by their size and matching maxillary articulation. They are distinctive in lacking projecting palatine shelves, and closely match corresponding elements of extant *Ceratophrys*. The maxilla (Fig. 3C and D) is exostosed except for the pars dentalis and had strong articulations with the premaxilla, nasal, squamosal, quadratojugal, and, presumably, neopalatine and pterygoid (not identified). Like the premaxilla, the anterior half of the maxilla lacks a palatal shelf. Teeth were present on the premaxilla (13 or 14 teeth) and maxilla (50–60 teeth), but are damaged. Their implantation resembles that of the nonpedicellate *Ceratophrys*. In one partial maxilla [FMNH (Field Museum of Natural History) PR 2506], sharp, monocuspid unankylosed tooth tips are preserved *in situ* in the broken tooth bases. The large nasals (Fig. 3E–G) are L-shaped, with a tapering rostral process, a long recurved maxillary process, and a short dorsomedial plate that was co-ossified with the sphenethmoid and covered it completely. Medially the nasals and frontoparietals both met their counterparts in a strong, hori-

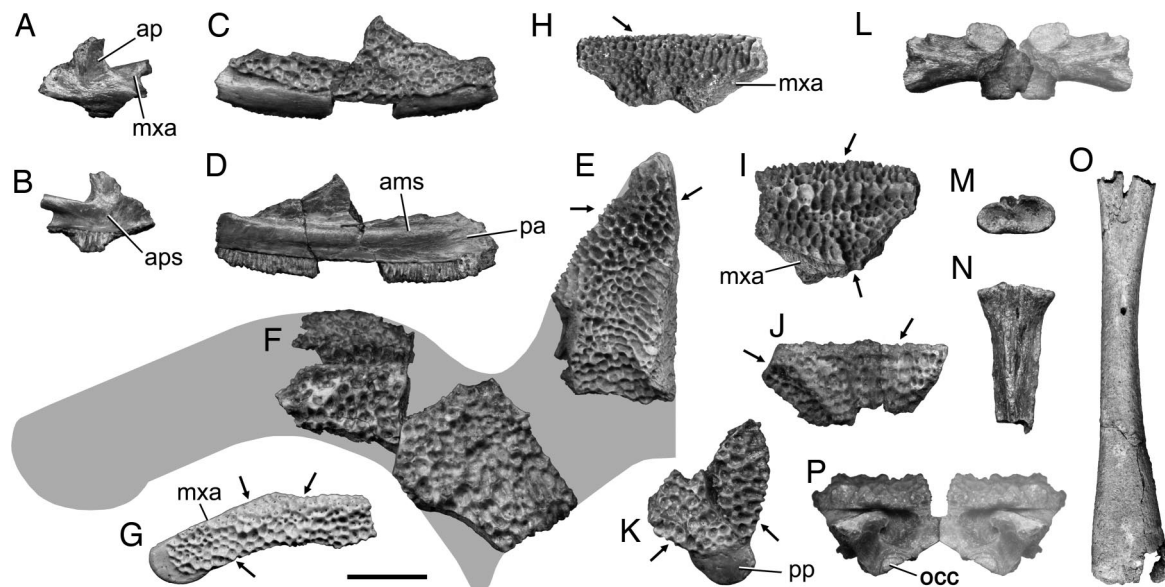


**Fig. 2.** *Beelzebufo ampinga*, Late Cretaceous of Madagascar. (A) Skull reconstruction showing parts preserved (white areas, *Left*) and distribution of pit-and-ridge ornament (stippling, *Right*). (B) Skeletal reconstruction and inferred body outline of average-sized (skull width, 200 mm; SVL, 425 mm) adult female *B. ampinga* based mainly on *Lepidobatrachus asper* (32). White areas indicate parts represented by fossil specimens. For size comparison, dorsal view silhouettes of *Ceratophrys aurita* (the largest extant ceratophryine) (C), and *Mantidactylus guttulatus* (the largest extant Malagasy frog) (D), are shown. cp, crista parotica; fm, foramen magnum; frp, frontoparietal; mx, maxilla; n, nasal; pmx, premaxilla; qj, quadratojugal; qu, quadrate; sq, squamosal. (Scale bars: 50 mm.)

zonally laminated suture. Posteromedially each frontoparietal (Fig. 3J) was fused to the underlying endocranium (UA 9675, Fig. 3P), but posterolaterally, the bone extended into a shelf that was separated from the crista parotica by a distinct posttemporal fenestra (25, 26). As preserved (UA 9640), the shelf is embayed posteriorly but less so than in *Ceratophrys*. It probably met the squamosal behind the orbit to form a parieto-squamosal bridge but the lateral tip of the bone has not been identified with certainty. The squamosals were triradiate, with a zygomatic ramus that was strongly sutured to the maxilla (Fig. 3H and I), a flange-like horizontal otic ramus (Fig. 3K) and, preserved only at the base, a ventrolateral ramus. Whether the zygomatic process of the squamosal met the nasal below the orbit is uncertain. The only nasal with a complete ventrolateral tip (UA 9680, Fig. 3G) suggests abutment rather than a suture, but the bone is from a juvenile and the relationship may have changed with maturity. A slender quadratojugal met the maxilla anteriorly and was co-ossified posteriorly with a robust mineralized quadrate (pars quadrata palatoquadrati).

The cervical vertebra (= atlas) is characterized by large, confluent anterior cotyles (Fig. 1*A*) [Type 3 (25)], and by fusion of its centrum to that of the second presacral (Fig. 1*B* and *C*), as in some large *Ceratophrys* (25). Known presacrals are procoelous. The sacral vertebra (Fig. 3*L*) is bicondylar posteriorly and has a dorsoventrally compressed diapophysis that is slightly flared distally (unlike the cylindrical diapophyses of ranids). The presence of an anterior cotyle rather than a condyle on the sacral centrum suggests that the last presacral was not biconcave, as it is in many ranoid anurans (16). The stout urostyle (Fig. 3*M* and





**Fig. 3.** Representative elements of *Beelzebubo ampinga*, Late Cretaceous of Madagascar. (A and B) Left premaxilla (UA 9622), labial and lingual views. (C and D) Left maxilla, anterior region (FMNH PR 2510), labial and lingual views. (E) Right nasal, rostral process (UA 9674), dorsal view reflected. (F) Partial left nasal (UA 9629), dorsal view, within scaled nasal shape. (G) Immature right nasal, maxillary process (UA 9625, reflected for comparison with F), dorsolateral view. (H) Right squamosal, maxillary process (FMNH PR 1959), lateral view. (I) Left squamosal, partial maxillary process (UA 9639), lateral view. (J) Left frontoparietal, anterior region (FMNH PR 2512), dorsal view. (K) Right squamosal, otic process (FMNH PR 2536), dorsal view. (L) Sacral vertebra, right half with left side added by reflection (FMNH PR 2003), dorsal view. (M and N) Urostyle, anterior part (UA 9636), anterior and dorsal views. (O) Left tibiofibula (UA 9628), posterior view. (P) Left frontoparietal and exoccipital in posterior view with right side added by reflection (UA 9675). Small arrows indicate unbroken edges. ams, absence of medial shelf; ap, alary process; aps, absence of palatal shelf; mxa, maxillary articulation; occ, occipital condyle; pa, premaxillary articulation; pp, posterior process. (Scale bar: 10 mm.)

*N*) has no transverse processes. The pelvis is represented by a partial right ilium (UA 9681) that lacks a dorsal crest, and the short, broad tibiofibula (Fig. 3O) resembles that of living anurans that are predominantly ambulatory.

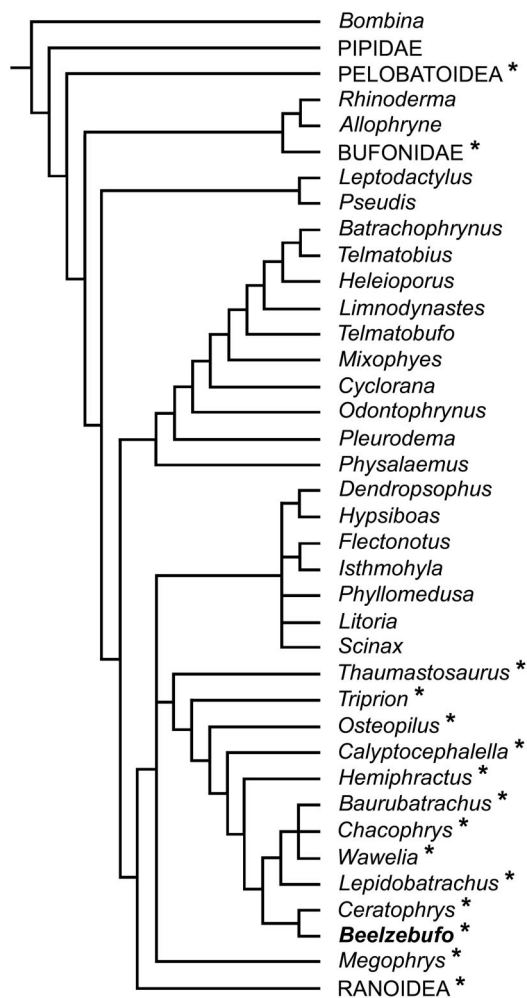
Unlike *Ceratophrys* and *Lepidobatrachus*, in which the skull bones co-ossify early, the sutures remained patent in the largest specimens of *Beelzebufo*, suggesting an enhanced potential for prolonged growth. Extant Ceratophryinae range in size from snout-vent length (SVL) 40–50 mm [*Chacophrys pierottii* (28)] to 170 mm [*Ceratophrys aurita* (29)]. Estimates based on extant taxa (SI Tables 1 and 2), indicate that most specimens of *B. ampinga* belonged to individuals with an estimated posterior skull width (Sk.W) of 80–120 mm (SVL 160–270 mm), but a few bones represent anurans of significantly larger size (Sk.W 150–200+ mm, SVL >400 mm, Figs. 2B and 3 E and F). In extant ceratophryines (29), the smaller, but more widely represented, size class consists of subadults and adult males; adult females are significantly larger. The size distribution in *Beelzebufo* suggests a similar pattern. The largest individuals would have dwarfed the largest extant ceratophryine, *Ceratophrys aurita* (Fig. 2C), and the largest extant Malagasy anuran (*Mantidactylus gutturalatus*) (Fig. 2D), rivaling Miocene representatives of *Calyptocephalella* sp. [= *Caudiverbera* (30)] from Argentina (31) and the extant West African *Conraua goliath*.

## Discussion and Conclusions

**Phylogenetic Position.** Taken together, the skeletal characters of *Beelzebufo* are consistent with neobatrachian affinity (25, 33). The characters of the vertebral column (procoely; sacro-urostylar articulation bicondylar; weakly dilated sacral diapophyses; no urostylar transverse processes) render attribution to leiopelmatids, bombinatorids, discoglossids, pipids, or pelobatoids (23, 24, 33) unlikely, and also exclude Cretaceous Asian gobiatines (34). Some characters (cranial exostosis; skull wider

than long; palatoquadrate mineralized, fused to quadratojugal; parieto-squamosal bridge; maxillary pars facialis large, with strong nasal, squamosal and quadratojugal articulations; cervical cotyles approaching one another in ventral midline, cervical and second presacral centra fused) occur, in different combinations, in hyperossified taxa from a range of lineages, including some pelobatoids, the hyloids *Calyptocephalella* and *Hemiphractus*, some hylids (e.g., *Triprion*, *Osteopilus*), some ranids (e.g., *Pyxicephalus*, *Aubria*, and *Ceratobatrachus*), and Ceratophryinae (24, 25, 33, 35) (see also [SI Text](#)). This hyperossification complicates comparison (35), but other characters constrain the possibilities. *Beelzebufo* lacks the derived vertebral characters of most ranoid anurans, and the basal hyloid *Calyptocephalella* lacks posttemporal fenestrae. The presence of maxillary teeth and large orbits differentiate *Beelzebufo* from the hyperossified Indian *Nasikabatrachus* (36, 37), although the latter's osteology remains largely undescribed. Conversely, a unique combination of skull characters (posterolaterally expanded frontoparietals, premaxilla strongly articulated with maxilla; premaxilla and anterior maxilla without palatal shelves) link *Beelzebufo* to Ceratophryinae (25), a small clade with three extant genera (*Ceratophrys*, *Lepidobatrachus* and *Chacophrys*) and two attributed fossils [*Baurubatrachus*: Late Cretaceous, 67–65 Mya, Argentina (27); *Wawelia*: Miocene, 14–12 Mya, Argentina (38)]. Other characters of *Beelzebufo* [teeth unicuspid; nasal body short and broad, with tapering rostral process; strong inter-nasal sutures; nasal with long, recurved maxillary process bearing rounded, unornamented tip; presence of posttemporal fenestrae; squamosal otic process prominent, horizontal; cervical cotyles confluent in ventral midline, Type 3 (25); ilium without prominent dorsal crest] are consistent with this attribution (25, 28, 32, 39), as are fragments of possible bony dorsal shield (UA 9619) (see [SI Text](#) for further comparison).

This hypothesis of ceratophryine relationship is supported by phylogenetic analysis (Fig. 4) that nests *Beelzebufo* within Cera-



**Fig. 4.** Seventy percent Majority Rule Consensus of 106 equally parsimonious trees (length, 633; consistency index, 0.3; rescaled consistency index, 0.169). Monophyletic clades not directly relevant to the discussion have been collapsed to single nodes. Asterisks denote that the clade, or part of it, contains exostosed and/or hyperossified taxa.

tophryinae, as the sister taxon of *Ceratophrys*, although this latter position may reflect the more generalized morphology of *Ceratophrys* in comparison with the derived *Lepidobatrachus* and paedomorphic *Chacophrys* (28, 32, 39). *Baurubatrachus* and *Wawelia* group together, sometimes with *Chacophrys*. Both South American fossil taxa show ceratophryine postcranial features [strongly elongated anterior presacral transverse processes, short urostyle (25, 32, 39)] but apart from a sculptured fragment, *Wawelia* lacks a skull and this problem limits comparison. As originally described (27), *Baurubatrachus* is more primitive than extant taxa and *Beelzebufo* in lacking a frontoparietal-squamosal bridge, and in having bicuspid teeth and a palatal shelf on the anterior maxilla. However, ongoing restudy suggests some of this information will change (A. Baez, personal communication). We also included *Thaumastosaurus* (Eocene, Europe) in our analyses as it has been discussed in relation to Ceratophryinae (40) but it was placed outside the group.

**Ecology.** Ceratophryinae are found today throughout South America, mainly in warm, seasonally dry habitats with ephemeral pools (28, 29). The environment of deposition of the Maevarano Fm was comparable (22), and *Beelzebufo* may have resembled *Ceratophrys* in being terrestrial, with a tendency to

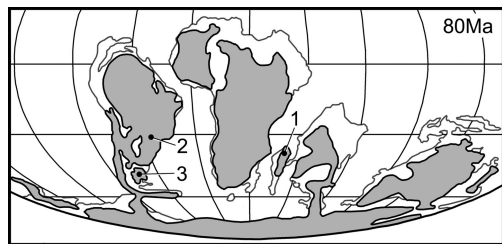
burrow [exostosis; thick, strongly sutured nasals (33)]. Ceratophryines are ambush predators that include vertebrates in their diet (29). Their strong bite is correlated with hyperossification, sharp teeth, and stabilizing connections between the upper jaw and skull (33). *Beelzebufo* has the same morphology, and large adults would have been formidable predators on small vertebrates.

**Biogeography and the Evolution of Malagasy Anura.** The fossil record of Gondwanan anurans is patchy. Pipoids dominate the South American record (31, 34), but hyloid neobatrachians are represented in the Late Cretaceous by *Baurubatrachus* and *Estesiella*, with bufonids and hylids reported from the Paleocene, and *Calyptocephalella* from the Oligocene onwards (31). Discoglossoids are recorded from the earliest Cretaceous of Morocco (41), but otherwise the African Mesozoic and early Tertiary record is limited to pipoids (34). Nothing is known from Antarctica, but the earliest Australian anuran (Eocene, 54.6 Mya) is attributed to the extant myobatrachid genus *Lechriodus*, with pelodyadine hylids and microhylids reported from the late Oligocene onward (42). The Late Cretaceous fauna of India reportedly combines Laurasian (gobioline discoglossoid, pelobatoid) and Gondwanan (hyloid, ranid-rhacophorid) elements (43). However, with the exception of the putative myobatrachid *Indobatrachus*, these records rely on incomplete ilia and are tentative.

Based on the distribution patterns of living and extinct taxa (but allowing for hyperoliid dispersal), the Cretaceous anuran fauna of the Madagascar–Seychelles–India Plate, or of parts of this plate after its fragmentation, would have included the ancestors of (i) endemic Malagasy taxa (mantellids; discophine, scaphiophryine and cophyline microhylids); (ii) endemic Seychellian taxa (sooglossids); and (iii) ancient Indian lineages (*Nasikabatrachus*; ranixaline, micrixaline, and nyctibatrachine ranids; rhacophorids), with the possibility of pipids, early African ranids, myobatrachids, and basal hylids (7, 12, 16–19, 31, 35, 44, 45). A ceratophryine is unexpected. In conventional paleobiogeographic models (e.g., 2), the Madagascar–Seychelles–India plate lost contact with the Antarctica/Australia landmass (and thus also South America)  $\approx 120$  Mya. However, an alternative hypothesis posits the existence of physical links between Madagascar, the Indian subcontinent, and South America that persisted late into the Late Cretaceous [ $\approx 80$  Mya (3)]. As early as 1927, paleontologists (46) noted similarities between the dinosaurs of these three regions, and the fossil assemblage of the Maevarano Fm provides further support, with the most striking links to the Indian subcontinent and South America involving theropod and sauropod dinosaurs, crocodyliforms, and mammals (1). The late persistence of a physical connection between Madagascar and southern Gondwana has also received support from molecular studies on ratite birds (47), and on iguanian lizards, podocnemid turtles, and boid snakes (48). The presence of a ceratophryine anuran, with South American relatives, in the Late Cretaceous of Madagascar provides strong and independent support for this paleobiogeographic reconstruction (Fig. 5).

**Hyloid Diversification.** An early molecular analysis (49) provided minimum age estimates of  $\approx 55$  Mya (early Eocene) for the origin of extant Ceratophryinae, and this result is reasonably consistent with the presence of Late Cretaceous ceratophryines in South America and Madagascar. However, more recent analyses have dated the divergence of *Ceratophrys* from *Lepidobatrachus* to the latest Oligocene or Miocene [12.7–26.1 (45, 50)], results that are clearly incompatible with the attribution of either *Baurubatrachus* or *Beelzebufo* to the crown group. Moreover, based on the relatively low levels of genetic divergence among extant hylids (45), some analyses also date the main hyloid radiation (i.e., without myobatrachids or *Calyptocephalella*) as occurring at, or





**Fig. 5.** Map showing positions and coastlines of the southern continents at 80 Ma (3) and indicating localities of *Beelzebufo* (position 1), *Baurubatrachus* (position 2), and *Wawelia* (position 3).

soon after, the Cretaceous–Paleogene boundary [65–55 Mya (confidence limits 52–84 Mya) (45, 50, 51)]. This finding is difficult to reconcile with the presence of ceratophryines (or even stem-ceratophryines) in Madagascar at 70–65 Mya, even allowing for confidence limits, as the island was isolated from at least 80 Mya (3).

Given that the estimated dates of hyloid origin [130–152 Mya, confidence limits, 108–208 Mya (7, 19, 36, 45, 51)] substantially predate those for the beginning of the main hyloid [nobleobatrachian (24, 45)] radiation [“long fuse” (45)], there is potential for some lineages to have arisen earlier. It is, of course, possible that *Baurubatrachus* and *Beelzebufo* are hyperossified stem-hyloids that are convergent on ceratophryines, but the skeletal evidence for ceratophryine affinity, at least for *Beelzebufo*, is compelling. The relationships of the component clades of “Leptodactylidae” (including ceratophryines) are still incompletely resolved (e.g., refs. 24, 35, 36, 45, 50, and 52). Ceratophryines have been alternately placed as basal hyloids (e.g., refs. 25, 53, and 54) or more deeply nested (e.g., refs. 18, 24, 35, and 36), and even their sister group is uncertain [e.g., telmatobines (24, 35), hyloids (36, 45), hemiphractines (50)]. This uncertainty makes it difficult to date their origin. Moreover, Ceratophryinae is a very small clade and thus resembles other such clades (e.g., sooglossids, *Heleophryne*, ranixalids, *Calyptocephalella*, *Rhinoderma*, centrolenids) posited to be remnants of older, formerly more widespread, lineages (44). Under this hypothesis, *Baurubatrachus* and *Beelzebufo* provide at least minimum constraints on the antiquity of Ceratophryinae.

**Conclusions.** We suggest that extant ceratophryines are remnants of a Gondwanan hyloid clade that once ranged from at least South America to Indo-Madagascar. Whether this clade was more broadly distributed and on which Gondwanan landmass it originated cannot be determined on current evidence. However, as the Late Cretaceous fauna of the Maevarano Fm (1, 4), including its ceratophryine anuran, bears little resemblance to that of modern Madagascar, major biotic changes clearly occurred on the island in the intervening period. When and how the

ancestors of the endemic mantellid and microhylid anurans arrived on Madagascar remains controversial (5, 6, 8, 12, 18, 19), but there is general agreement that these frogs did not diversify significantly until the Paleogene (5, 6, 12, 18, 19). Their radiation has been linked, at least in part, to the expansion of rainforests, but may also have been facilitated by the extinction of archaic faunal elements (5), including ceratophryines.

## Methods

*Beelzebufo*, *Baurubatrachus*, and *Wawelia* were coded into an existing morphological character matrix (39) with 81 characters and 62 taxa including “basal” anurans (*Bombina*, pipids, pelobatoids) and ranoid and hyloid neobatrachians. Some genera were originally represented by several species, but these taxa were run as single, sometimes polymorphic, units to make the analysis more manageable. The matrix was then extended to broaden the sampling of microhylids, myobatrachids, and hyperossified taxa (see *SI Text* for character list and details; see *SI Table 3* for matrix). Parsimony analysis was performed by using PAUP version 4.01b (55) in heuristic search mode (because of matrix size), with default settings (but multistate characters coded as polymorphism). *Bombina* (Bombinatoridae); *Xenopus* and *Hymenochirus* (Pipidae); and *Megophrys*, *Pelobates*, *Spea* and *Scaphiopus* (Pelobatoidea) were designated outgroups. This analysis resulted in 106 equally parsimonious trees [length (L), 633; consistency index (CI), 0.3; rescaled consistency index (RC), 0.169]. The full topology (70% majority rule tree) is shown in *SI Fig. 9*. In *Fig. 4*, pipids, pelobatoids, bufonids, and ranoids are collapsed to single nodes. The overall tree topology shows some similarities with previous analyses (and anomalies, e.g., the positions of bufonids and *Megophrys*) although, as for other morphological trees (e.g., refs. 35 and 39), and in contrast to most molecular analyses (e.g., refs. 24, 35, 36, 45, and 52), Hyloidea does not form a monophyletic sister taxon to Ranoidea. Additionally, as highlighted by others (35), characters relating to size and cranial hyperossification can have a disproportionate effect (e.g., the placement of *Calyptocephalella* and the hyloids *Osteopilus* and *Triprion*, close to ceratophryines, rather than with less ossified relatives). We reran the analysis using a subset of 18 exostosed and/or hyperossified taxa (Branch and Bound search, characters unordered and unweighted; multistate characters treated as polymorphism). This analysis yielded nine maximum parsimony trees (L, 168; CI, 0.565; RC, 0.307) in which ceratophryines, including *Beelzebufo*, *Baurubatrachus*, and *Wawelia*, consistently grouped together (*SI Fig. 10*). In a bootstrap analysis (1,000 replicates) run on the same dataset, support values for most clades were low.

Size was estimated by comparing *Beelzebufo* bones with equivalent elements from *Ceratophrys* and *Calyptocephalella*, using a range of specimens from juvenile (Sk.W = 44 mm) to full adult (Sk.W = 98 mm) to allow for allometry (see *SI Tables 1 and 2*).

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